On the correct placement of *Erebia epipsodea* Butler, 1868 within the genus *Erebia* Dalman, 1816 (Lepidoptera: Satyridae)

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Abstract. It is demonstrated that the Nearctic species *Erebia epipsodea* Butler, 1868 is the closest relative to the Palaearctic species *Erebia medusa* (Denis & Schiffermüller), [1775] and has no affinity with the species of the *Alberganus* group, in which it was placed previously. This conclusion is suggested by certain details of the male genitalic structure, but is confirmed by the structure of the female genitalia. Therefore *E. epipsodea* is removed from the *Alberganus* species group and placed into the *Medusa* group of species.

Since the time of the original description, the position of *Erebia epipsodea* Butler, 1868 within the system of the genus *Erebia* Dalman, 1816 was not stable. While describing it, Butler (1868) has clearly stated that the new species is very similar to *Erebia psodea* (Hübner, 1804): "Alae supra forma et coloribus fere Psodeae (Hbn.)... Alae anticae subtus velut in Psodea sed magis rufescentibus...". In contrast to the explanation in Bird et al. (1995), the specific epithet "epipsodea" is given exactly in this connection: "epi" in Greeks means "on", "towards" and "psodea" is [at present] the name of a Southeast European subspecies of *Erebia medusa* (Denis & Schiffermüller), [1775]. In the time of Butler the name *Erebia psodea* (Hübner, 1804) was in common usage for the species called at present *Erebia medusa* (Denis & Schiffermüller), [1775].

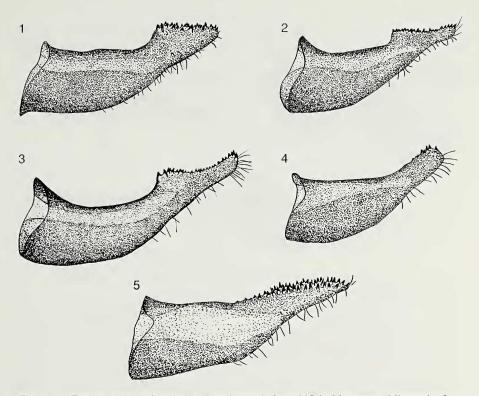
When the structure of the male genitalia of *E. epipsodea* and *E. medusa* was studied and compared, the first species was placed far from the second one on the basis that the male genitalia of both species look quite different (Chapman 1898). Chapman divided the genus *Erebia* into two sections and nine groups. *E. medusa* was placed in the section "A" group "VII"; *E. epipsodea* in section "B" group "VIII".

However, even knowing this, at the same time Elwes again placed *E. epipsodea* near *E. medusa* as its closest relative, basing this on the clear external similarity of both species (Elwes 1898).

Warren refuted this point of view in his monumental work on the genus *Erebia* (Warren 1936). He divided the genus into 15 specific groups, placing both discussed species in different groups, taxonomically distant from each other. *E. medusa* was placed into "IX. *Medusa* Group" while *E. epipsodea* was placed into "XI. *Alberganus* Group".

Warren (1936) had noticed very characteristic features in the genitalia of *E. epipsodea*: branches of juxta heavily chitinized and covered with teeth,

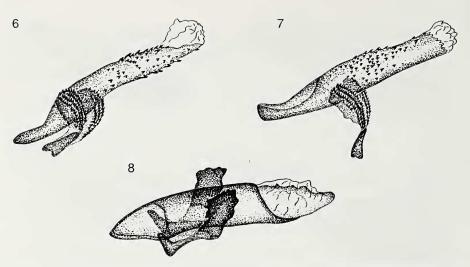
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- Fig. 1. *Erebia epipsodea*: left valva, lateral view. USA, Montana, Missoula Co., Miller Creek, 12.VI.1982, S. Kohler *leg*.
- Fig. 2. *Erebia theano*: left valva, lateral view. Canada, Manitoba, Churchill, 20.VII.1981, P. Klassen *leg*.
- Fig. 3. *Erebia alberganus*: left valva, lateral view. Switzerland, Wallis, NE Hohtenn/Lonza, Alp Tatz - Alp Laden, 11.VII.1977, C. Häuser *leg*.
- Fig. 4. *Erebia medusa*: left valva, lateral view. Russia, Chita region, Yablonovyy mountain range, vic. Yablonovo, 20.VI.1995, A. Belik *leg*.
- Fig. 5. *Erebia kozhantshikovi*: left valva, lateral view. Russia, Yakutia, Oymiakon distr., vic. Ust'-Nera, 25.VI.1993, S. Sazonov *leg*.

and coarse teeth on the aedoeagus (Fig. 6). He noted that the presence of these structures makes *E. epipsodea* a unique species within the whole genus. However he was certainly disoriented by two things. First is the general superficial similarity of the form of the valvae in *E. epipsodea* male genitalia (Fig. 1) to those of the species of the *Alberganus* group. Though not exactly resembling any species of the *Alberganus* group, the outline and comparative sizes of valvae elements in *E. epipsodea* are especially similar to those of some Nearctic representatives of *E. theano* (Tauscher, 1806) (Fig. 2). For the comparison, the shape of the valvae of *E. alberganus* is also shown here (Fig. 3). Second is the clearly considerable difference in the form of the valvae between the genitalia of *E. epipsodea* and of *E. medusa* (Fig. 4).

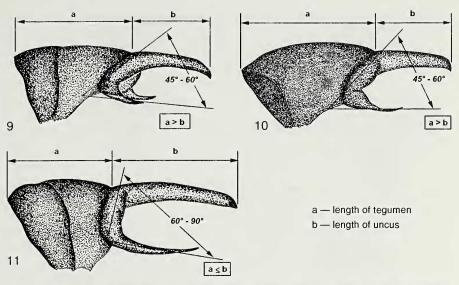
After the exhaustive work of Warren (1936) there were no further attempts

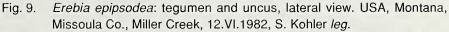


- Fig. 6. *Erebia epipsodea*: aedoeagus and juxta, lateral view. Canada, Manitoba, Riding Mountains, 21.VI.1982, P. Klassen *leg*.
- Fig. 7. *Erebia medusa*: aedoeagus and juxta, lateral view. Russia, Chita region, Yablonovyy mountain range, vic. Yablonovo, 20.VI.1995, A. Belik *leg.*
- Fig. 8. *Erebia alberganus*: aedoeagus and juxta, lateral view. Switzerland, Wallis, NE Hohtenn/Lonza, Alp Tatz Alp Laden, 11.VII.1977, C. Häuser *leg*.

at critical revision of the genus *Erebia*. Kurentzov (1970), reviewing systematics and distribution of the genus *Erebia* both in the Eastern Palaearctic and partly in the Nearctic region, mentioned *E. epipsodea* as a member of the *Alberganus* species group. Later there were two publications by Japanese authors. First of these publications was the paper of Murayama (1975), which was a brief illustrated abstract of Warren's "Monograph of the genus *Erebia*" rather than a new critical review of the genus. Published recently was the well illustrated work of Kogure & Iwamoto (1992; 1993). In both these papers *E. epipsodea* was also placed into the *Alberganus* species group, though the latter authors stated: "This species is placed in Group XI, *Alberganus* group because of structural characteristics of the male genitalia, but its morphological characteristics such as the size and the pattern of the wings are similar to those of *E. medusa*" (Kogure & Iwamoto 1993).

The question about a close relationship between *E. medusa* and *E. epipsodea* was raised again by Pringle (1992). It is demonstrated in that article that male genitalia of *E. medusa* have the same characteristic features that Warren (1936) considered as unique for *E. epipsodea*. The branches of the juxta are heavily chitinized and covered with teeth, and there are well developed teeth on the aedoeagus (Fig. 7). For the comparison, the aedoeagus and the juxta of *E. alberganus* are also illustrated here (Fig. 8) to show the shape of these structures in members of the *Alberganus* group. The author's study of specimens of *E. medusa* from various localities (from West Europe to Transbaikal Siberia) has confirmed the data reported by Pringle (1992) [Note: in all examined species the vesica is without cornuti]. Warren seems



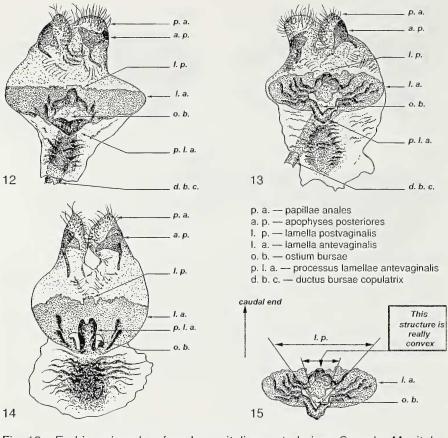


- Fig. 10. *Erebia medusa*: tegumen and uncus, lateral view. Russia, Chita region, Yablonovyy mountain range, vic. Yablonovo, 20.VI.1995, A. Belik *leg.*
- Fig. 11. *Erebia alberganus*: tegumen and uncus, lateral view. Switzerland, Wallis, NE Hohtenn/Lonza, Alp Tatz Alp Laden, 11.VII.1977, C. Häuser *leg*.

to have completely overlooked these important details in the male genitalia of *E. medusa*.

Studying the morphology of various species of Erebia, the author has noticed that the male genitalia of E. epipsodea and E. medusa have two other similar features, which at the same time distinguish E. epipsodea from all species of the Alberganus group. Sometimes these features are not clearly developed, but on material from series it is quite notable. The first feature is the comparative length of uncus and tegumen. In E. epipsodea and E. medusa the uncus is shorter than the tegumen (Figs. 9-10), in species of the Alberganus group the uncus is of equal length to the tegumen or even somewhat longer (Fig. 11). The second feature is that both in E. epipsodea and E. medusa the uncus with gnathos is connected to the tegumen with a rather acute angle, which varies from near 45° to 60° (Figs. 9-10). In members of the Alberganus group the uncus with gnathos is connected to the tegumen with a less acute angle, from 60° to 90° (Fig. 11). Numerous examples of these facts may be observed in the figures of Warren (1936: Figs. 334-338, 357-385); more examples of male genitalia of some North American species of the Alberganus group are shown by Troubridge & Philip (1983: Figs. 46-51).

However, all the mentioned features (phenetic similarity of *E. epipsodea* with *E. medusa* and notable external difference of *E. epipsodea* from all species of *Alberganus* group; the same features in male genitalic structures of



- Fig. 12. *Erebia epipsodea*: female genitalia, ventral view. Canada, Manitoba, Riding Mountains, 5.VI.1977, P. Klassen *leg.*
- Fig. 13. *Erebia medusa*: female genitalia, ventral view. Russia, Chita region, Yablonovyy mountain range, vic. Yablonovo, 20.VI.1995, A. Belik *leg.*
- Fig. 14. *Erebia alberganus*: female genitalia, ventral view. Switzerland, Wallis, NE Hohtenn/Lonza, Alp Tatz Alp Laden, 11.VII.1977, C. Häuser *leg*.
- Fig. 15. *Erebia medusa*: sterigma (female genital plate), ventral view. Russia, Chita region, Yablonovyy mountain range, vic. Yablonovo, 20.VI.1995, A. Belik *leg*.

E. epipsodea and *E. medusa*, which are lacking in the male genitalia of species of the *Alberganus* group) seem to be not quite enough to remove *E. epipsodea* from the Alberganus group and to place it into *Medusa* group. There is still the shape of the valvae in the male genitalia of *E. epipsodea*, which is not consistent with the idea of the affinity of *E. epipsodea* with *E. medusa*.

The author believes that the form of the valvae in male genitalia within the genus *Erebia* is a less stable trait, more subjected to adaptive radiation and specialization during the evolutionary process of speciation. For example, *E. kozhantshikovi* Sheljuzhko, 1925 undoubtedly belongs to the *Alberganus* group, but the form of the valvae (Fig. 5) may be very different from the generalized shape of valvae in this group. At the same time the form and comparative sizes of the uncus and tegumen, and the form and chitinization of the juxta and aedoeagus seem to be much more conservative. So in certain cases the intrageneric arrangements of Warren, when based primarily on the form of the valvae, are not natural.

The author's study of the comparative morphology of female genitalia in the genus *Erebia* has revealed new and indisputable proof that *E. epipsodea* belongs to the *Medusa* group and has no relationship to the *Alberganus* group.

The female genitalia of E. epipsodea (Fig. 12) are very similar to those of E. medusa (Fig. 13). Both species have a structure in the female genitalia the shape of which is very uncommon for the genus Erebia as a whole: a very short flat triangular process associated with lamella antevaginalis (processus lamellae antevaginalis), which is directed anteriorly. Therefore, the ostium bursae opens freely to the ventral side. In females of most species of the genus Erebia that were studied by the author, and in members of the Alberganus group in particular, the processus lamellae antevaginalis (of varying form, usually bifurcated at the distal end) is well developed. It is directed caudally and therefore covers the ostium bursae from the ventral side. This is illustrated for the case of E. alberganus (de Prunner, 1798) (Fig. 14); other members of Alberganus group have female genitalia of similar shape. Furthermore, in the female genitalia of E. epipsodea and E. medusa the lamella postvaginalis has a characteristic convexity (Figs. 12-13, 15), while in species of the Alberganus group the lamella postvaginalis is quite flat (Fig. 14). [Note: the author believes that the structure of the bursa copulatrix has no significant taxonomic value for the intrageneric systematics of the genus Erebia. In all species examined, it has the same structure (with two signa, identical in all species). Therefore the bursa copulatrix is not illustrated on Figs. 10-13.]

CONCLUSION

Summarizing the preceding argument, it is clear that the Nearctic species *E. epipsodea* is the closest relative of the Palaearctic species *E. medusa*, having no affinity with members of the *Alberganus* group. So herein *E. epipsodea* is removed from the *Alberganus* species group and placed into the *Medusa* species group of the genus *Erebia*.

APPENDIX: MATERIAL EXAMINED AND THE RANGE OF VARIATIONS

The conclusions presented in this paper, to be meaningful, could not be based merely on the study of single specimens. During the preparation of the present paper, genitalia were examined of a representative series of specimens from each discussed species and, for completeness of comparison, from all species of the *Alberganus* group:

Erebia epipsodea: 108, 59; from Idaho, Wyoming, Montana and Manitoba.

- *Erebia medusa*: 178, 79; from Norway, Austria, Italy, Bulgaria, Ukraina, Cisbaikal Siberia and Transbaikal Siberia.
- *Erebia alberganus*: 103, 69; from France and Switzerland.
- Erebia maurisius (Esper, 1803): 58, 19; from Altai and East Sayan Mtns.
- Erebia theano (Tauscher, 1806): 378, 139; from Altai, East Sayan Mtns.,
 - Yakutia, Magadan region, Yukon, Manitoba, Montana, Wyoming, Colorado.
- Erebia youngi Holland, 1900: 23 from Yukon;
- *Erebia dabanensis* Erschoff, 1871: 203, 49; from Polar Ural Mtns, Putorana Plateau, East Sayan Mtns. and Magadan region.

Erebia anyuica Kurentzov, 1966: 133, 29; from East Sayan Mtns. and Yakutia. *Erebia occulta* Roos & Kimmich, 1983: 43, 29 from Yukon.

Erebia kozhantshikovi Sheljuzhko, 1925: 58, 29 from Yakutia.

Erebia lafontainei Troubridge & Philip, 1983: 28 from Alaska.

A number of non-critical individual variations were seen in the genitalic structures of all above-mentioned species. In the male genitalia, these individual variations affect mainly the form of the valvae, while in the female genitalia they affect the general shape of the sterigma and the form of the processus lamellae antevaginalis.

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LITERATURE CITED

- BIRD, C.D., HILCHIE, G.J., KONDLA, N.G., PIKE, E.M., SPERLING, F.A.H. 1995. Alberta Butterflies. Edmonton, The Provincial Museum of Alberta, VIII+349 p.
- BULTER, A.G. 1868. Catalogue of the diurnal Lepidoptera of the family Satyridae in the collection of the British Museum. London, printed by order of the Trustees, 211 p.
- CHAPMAN, T.A. 1898. A review of the genus *Erebia*, based on an examination of the male appendages. Transactions of the Entomological Society of London 1898: 209–239.
- ELWES, H.J. 1898. A revision of the genus *Erebia*. Transactions of the Entomological Society of London, 1898:169–207.

- KOGURE, M. & IWAMOTO, Y. 1992. Illustrated catalogue of the genus *Erebia* in color. Yadoriga 150:2–33 [in Japanese].
- KURENTZOV, A.I. 1970. The butterflies of the far east USSR. Leningrad, "Nauka" Publishing House, 164 p., 14 pl. [in Russian].
- Murayama, S. 1975. A general view of the genus *Erebia* in the world. Gekkan-Mushi 54:9–14; 56:3-9; 57:3–6 [in Japanese].
- PRINGLE, G. 1992. A note on the Satyrid butterflies, *Erebia medusa* (D.& S.) and *Erebia epipsodea* Butler. British Journal of Entomology and Natural History 5:15–16.
- TROUBRIDGE, J.T. & PHILIP, K.W. 1983. A review of the *Erebia dabanensis* complex (Lepidoptera: Satyridae), with descriptions of two new species. Journal of Research on the Lepidoptera 21(2):107–146.
- WARREN, B.C.S. 1936. Monograph of the genus *Erebia*. London, printed by order of the Trustees, Adlard and Son Ltd., VII+407 p., 104 pl.